

Sweetgum Dormancy Release: Effects of Chilling, Photoperiod, and Genotype

By

ROBERT E. FARMER, Jr.

Southern Forest Experiment Station, Forest Service, U.S. Department of Agriculture
Southern Hardwoods Laboratory, Stoneville, Mississippi

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Abstract

In *Liquidambar styraciflua* L., 1200 to 1600 hours of chilling (3°C) resulted in rapid resumption of growth under greenhouse forcing conditions. Long photoperiods were effective substitutes for chilling. Plants from southern Alabama (Lat. 31°) had a lower chilling requirement than those from western Tennessee (Lat. 36°). Growth rate of plants under long photoperiod varied directly with degree of previous chilling.

Introduction

Dormancy in woody plants of the temperate zone, the subject of considerable recent research and review (Smith and Kefford 1964, Romberger 1963, Vegis 1964), is currently believed to be governed by a complex, environmentally controlled growth-regulator system. The dormant state can be induced by short-day photoperiods operating through the phytochrome system (Downs 1962). Under natural conditions dormancy is released in most species by a period of chilling. Effects of incomplete chilling may include both delayed budbreak and abnormal growth (Chandler *et al.* 1937, Romberger 1963).

Numerous studies of chilling requirements have been conducted with horticultural species (Weinberger 1961), and some forest tree species have received recent attention (Farmer 1964, Kriebel and Wang 1962, Roberts and Main 1965, Nienstaedt 1966, 1967). Distribution of chilling periods as well as total chilling time may be of importance (Bennett 1950, Overcash and Campbell 1955, Weinberger 1954, 1961). Genetic variation in chilling requirements has been demonstrated in a number of genera including *Acer* (Kriebel and Wang 1962, Perry and Wang 1960), *Picea* (Nienstaedt 1967, Worrall and

Mergen 1967), *Tsuga* (Olson, Stearns, and Nienstaedt 1959⁹), and *Prunus* (Weinberger 1961).

In many species dormancy may be released by long photoperiods, as well as by chilling (for examples, see Kramer 1936, Nienstaedt 1966, Olmsted 1951, Wareing 1951). Erez, Samish, and Lavee (1966) have published evidence that the phytochrome system is involved in this photoperiodically induced release. Gibberellins may also be substituted for chilling in some species (Donoho and Walker 1957, Romberger 1963).

In short, dormancy release is the result of photoperiod or chilling, or both, acting upon a genetically variable regulator system. The two greenhouse studies described in this article were undertaken to quantify effects of photoperiod, chilling, and genotype upon budbreak and subsequent growth of juvenile sweetgum. Specifically, the response of open-pollinated progenies from two geographical sources was observed under long, natural, and short photoperiods after various chilling periods. The work was done at Stoneville in west-central Mississippi.

Methods and Results

Experiment No. 1: — This test was undertaken in 1964 to observe the budbreak response, under natural winter photoperiods (10–11 hours), of seedlings given constant and interrupted chilling. In late November, seedlings of five open-pollinated trees from western Tennessee (Lat. 36°) and of five southern Alabama (Lat. 31°) trees were lifted from nursery beds at Stoneville and potted in loam.

Each family was represented by 33 seedlings. At lifting, plants were 6 months from seed and 25 to 45 cm high. They had received 160 hours of outdoor chilling (temperature below 7°C) interspersed by periods of warmer temperature and were still foliated.

Three seedlings from each family were immediately placed in the greenhouse for forcing; the remaining plants were placed in cold storage (3°C) under a 10-hour photoperiod maintained with incandescent lighting. During storage, one-half of the plants in each family were temporarily removed from storage at 10-day intervals and kept at 24°C for 30 hours. At 20-day intervals, six plants from each family were moved from storage to the greenhouse for forcing; three of these plants had received constant chilling, the other three received chilling broken by 30-hour warm periods.

During forcing, plants were arranged randomly on greenhouse benches and watered daily. Greenhouse temperature averaged 24°C and ranged from 18 to 32°C. Thermograph records revealed no evidence that chilling treatments were confounded with changes in greenhouse temperature.

Plants were observed daily and the date of initial budbreak recorded for each. The unit of analysis was number of days from the day plants were placed in the greenhouse (forcing date) to budbreak date. Effects of degree of chilling, type of chilling, geographic source, families within source, and factor interactions were tested at the 0.05 level of probability in a factorial type of variance analysis. Presumably because their chilling requirements were unsatisfied, many of the seedlings forced in November failed to resume

Table 1. Number of days from forcing date to budbreak after chilling at various levels. Experiment No. 1. Interruption every 10 days.

Source and type of chilling	Hours of chilling treatment					
	160	640	1120	1600	2080	2560
<i>Tennessee sources</i>						
A. Constant						
Average	93+ ¹	38	25	18	16	12
Family range	—	36-40	20-27	15-19	14-17	10-13
B. Interrupted by 30-hour warm periods						
Average	—	46	27	20	16	11
Family range	—	40-60	24-31	19-21	12-18	9-14
<i>Alabama sources</i>						
A. Constant						
Average	54+ ¹	32	20	15	13	9
Family range	—	29-36	17-24	13-16	10-16	7-10
B. Interrupted by 30-hour warm periods						
Average	—	34	23	17	12	8
Family range	—	29-40	22-26	14-19	10-16	7-10

¹ Mean based on incomplete data since one or more plants did not break dormancy during test period.

growth; data from this group of plants were therefore not included in the formal analysis.

Number of days to budbreak decreased rapidly with each increment of chilling time up to 1600 hours (Table 1); response to further chilling was less dramatic. Forty-three per cent of the plants forced in November after 160 hours' outdoor chilling had not resumed growth as of March 30, 1965, the last observation date; tabulated figures for this chilling period are therefore based on incomplete data.

Plants subjected to interrupted chilling for 160, 640, 1120, and 1600 hours responded more slowly to forcing than did continuously chilled plants. After 1600 hours there was no significant difference between the two treatments, but plants given interrupted chilling broke buds about 1 day earlier than constantly chilled material. A regression of days to budbreak over total hours' chilling for the two treatments revealed no difference between treatments after 600 hours' chilling. (Total hours = number of hours during which plants were at temperatures below 7°C. For interrupted chilling, this was less than total treatment time.)

After all chilling periods, seedlings from south Alabama resumed growth earlier than those from Tennessee. Within-source familial variation in budbreak response (Table 1) was also statistically significant and was influenced by chilling time; some changes in rank of family means were effected by chilling.

Experiment No. 2: — In 1965, the line of investigation initiated in the first experiment was continued with seedlings of 10 families continuously chilled and grown under long and short photoperiods. Stratified seed was sown

during June in loam-filled pots. Plants grew outdoors in family blocks for the remainder of the season; by mid-October apical buds were set.

In early November each family was divided into five groups of four plants each; mean heights of all groups were approximately equal within families. Each group was assigned to one of five chilling treatments: 0, 600, 1200, 1800, or 2400 hours at 3°C. Chilling was again in a cold storage room under a 10-hour photoperiod. Plants were foliated when placed in storage, but lost leaves during chilling. Unchilled plants were defoliated by hand prior to forcing. After chilling treatments, which began on November 10, plants were placed in the same greenhouse used for Experiment No. 1. Two plants from each four-plant family group were grown under a 16-hour photoperiod maintained by supplementing natural light with incandescent and fluorescent light. The other two plants were placed under a 9-hour photoperiod regime (the bench on which the pots were placed was covered with light-tight black polyethylene after the trees had received 9 hours of daylight). Plants were arranged randomly in both regimes.

Greenhouse environmental control was the same as for Experiment No. 1; mean temperature was approximately the same as in 1964. While temperature means under the two photoperiods were equal, temperatures under the long-day regime were slightly more variable than under the short-day regime, where the bench enclosure had a moderating effect at night.

Observations of individual seedlings included initial height, budbreak date, and height increment. The latter was recorded at 30-day intervals during the 90-day period following removal from cold storage. (Plants forced during the early phase of the test were measured up to 150 days.) Days from forcing to initial budbreak were analyzed as in Experiment No. 1; the analysis included only data from 1200-, 1800-, and 2400-hour chilling treatments, since some plants given less chilling did not break dormancy in the short-day regime. Mean daily apical growth was calculated for the period beginning with budbreak and ending 90 days after forcing date. Growth data were subjected to both an analysis of variance and an analysis of covariance with original seedling height as the independent variable. Factors were tested at the 0.05 level of probability.

Budbreak. — With the exception of Alabama seedlings under long days, increments of chilling caused an increase in rapidity of budbreak until plants received about 1200 hours of cold; thereafter chilling effects decreased (Table 2). Seedlings under long days responded more rapidly than those under short days. In the 400- and 800-hour treatments, in fact, many of the plants under the short photoperiod never broke dormancy. Effects of day-length decreased, however, when chilling periods exceeded 1200 hours. In Experiment No. 1, response of plants forced under natural day-lengths after partial chilling was intermediate relative to plants under long and short days in Experiment No. 2; results of the two tests are not strictly comparable, however.

Alabama material again responded more rapidly to the forcing environments than material from Tennessee. Under short days, plants from the two geographic sources responded similarly. Under long days, Tennessee plants chilled 0 to 600 hours broke dormancy in 36 to 38 days, then responded more rapidly after further chilling. Their reaction was similar to Tennessee plants

Table 2. Days from forcing date to budbreak as affected by chilling, day length, and seed source (Experiment 2).

Source and Photo-period (h)	Hours of chilling				
	0	600	1200	1800	2400
<i>Tennessee Sources</i>					
16	36+ ¹	38	24	17	19
9	154+ ¹	125+ ¹	38	23	29
<i>Alabama Sources</i>					
16	20	19	19	13	10
9	114+ ¹	71+ ¹	28	18	12

¹ Mean based on incomplete data since one or more plants did not break dormancy during test period.

in Experiment No. 1. Alabama seedlings, on the other hand, broke dormancy in 20 days or less after all degrees of chilling and exhibited little response to chilling increments. Within-source family variation was similar to that observed in the first experiment.

Growth. — Apical growth rate of plants under long days increased significantly with degree of chilling over the whole range of chilling treatments (Figure 1). Unchilled plants made very little growth and generally reset apical buds within 90 days after being forced. Under long photoperiods, plants in the remainder of the chilling treatments continued growing beyond the 90-day period, though many eventually reset buds (120 to 150 days after forcing date). They were growing continuously during the measurement period. Thus, with the exception of unchilled plants under long days, growth differences due to chilling are primarily those of rate.

Plants placed under the short photoperiod after 0 and 600 hours' chilling made essentially no apical growth. The few that broke dormancy within 90 days after the forcing date (Alabama material chilled 600 hours) grew

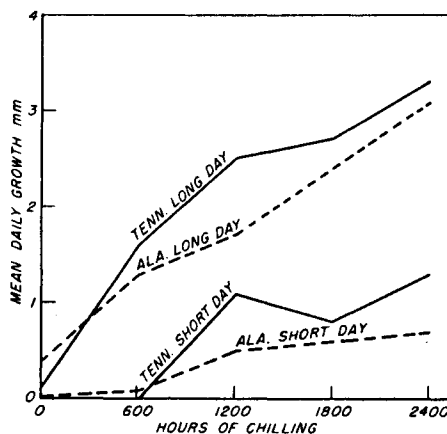


Figure 1. Relationship between chilling and subsequent mean daily growth under two photoperiods during the 90-day period following forcing date.

less than 0.5 cm before resetting apical buds. Plants chilled longer grew for a longer time under short days, but all reset apical buds within 60 to 90 days. Reduced duration of growth under short photoperiods thus accounts for most of the growth differences between long- and short-day regimes. Effects of chilling upon the short-day plants are likewise at least partly reflected in differences in growth duration.

Effects of geographic source were nonsignificant for growth rate, but families within sources had means for all treatments ranging significantly from 0.8 to 1.9 mm per day. Families also varied in their reaction to chilling increments; there was a statistically significant chilling \times family interaction. As with budbreak, this interaction was due to family ranking changes effected by chilling.

Discussion

Dormancy release of juvenile sweetgum as observed in this study was a function of chilling, forcing photoperiod, and genotype. Continuous chilling for 1200 to 1600 hours resulted in normal budbreak of plants from both geographical sources under any day length. After this amount of chilling, plants can be considered in a state of imposed dormancy although, as noted by Romberger (1963), the end point of physiological dormancy can probably not be sharply fixed in time.

Long photoperiods were effectively substituted for chilling in breaking dormancy, as noted previously for sweetgum by Kramer (1936). In addition, less dramatic but consistent day-length effects occurred after all levels of chilling, suggesting that photoperiod may have some influence during all phases of dormancy.

Genetic effects attributable to geographic source were qualitatively similar to those reported for other species (Kriebel and Wang 1962, Perry and Wang 1960, Nienstaedt 1967). On the average, plants from Tennessee required from 200 to 600 hours more chilling than Alabama seedlings to respond with equal rapidity to forcing. However, family differences within sources were frequently larger than source differences. It is also notable that, given a long photoperiod, chilling had little effect upon budbreak in the southern plants.

The study provided no evidence that chilling broken at 10-day intervals by warm periods resulted in true dormancy reinduction, although continuously chilled plants broke buds a few days earlier than intermittently chilled ones early in the test. This observation is, in principle, contradictory to data on dormancy reinduction by Bennett (1950), Overcash and Campbell (1955), and Weinberger (1954), but treatment differences probably account for the variance. These investigators subjected plants to diurnal temperature fluctuations beginning early in dormancy. Other evidence (Weinberger 1961) indicates that fewer total hours' chilling may be required for material subject to temperature fluctuations than for material constantly chilled. Moreover, chilling at the beginning of the dormant period may be more effective than chilling in late winter (Brown 1957). As noted by Nienstaedt (1966), diurnal fluctuations in late autumn temperatures may have a reinductive effect. At present no definitive statement can be made regarding effects of temperature

fluctuations upon chilling requirements. Separate experimental consideration of 1) initial chilling date, 2) amount and distribution of chilling time, and 3) time *per se* may be requisite to a full understanding of dormancy release.

The response of apical growth to chilling increments supports the hypothesis that degree of chilling is positively related to subsequent growth. This relationship was also influenced by photoperiod: Growth rate varied almost linearly with chilling under long photoperiods; under short days, rapid resumption of dormancy masked any difference in rate which may have existed. A minimum of 600 hours' chilling was required to prevent even plants under long days from resetting apical buds after a short period of growth. These results with trees from both sources indicate that some chilling is required for normal short-term growth under long-day greenhouse conditions.

Present address of the author: Division of Forestry, Development, Tennessee Valley Authority, Norris, Tennessee.

References

- Bennett, J. P.: Temperature and bud rest period. Effect of temperature and exposure on the rest period of deciduous plant leaf buds investigated. — *Calif. Agr.* 4(1): 11, 13, 15-16. 1950.
- Brown, D. S.: The rest period of apricot flower buds as described by a regression of time of bloom on temperature. — *Plant Physiol.* 32: 75-85. 1957.
- Chandler, W. H., Kimball, M. H., Philip, G. L., Tufts, W. P. & Weldon, G. P.: Chilling requirements for opening buds of deciduous orchard trees and some other plants in California. — *Calif. Agr. Exp. Sta. Bull.* 611. 1937.
- Donoho, C. W., Jr. & Walker, D. R.: Effect of gibberellic acid on breaking of rest period in Elberta peach. — *Science* 126: 1178-1179. 1957.
- Downs, R. J.: Photocontrol of growth and dormancy in woody plants. — *In Tree Growth* (T. T. Kozlowski, ed.), pp. 133-148. Ronald Press, New York. 1962.
- Erez, A., Samish, R. M. & Lavee, S.: The role of light in leaf and flower bud break of the peach (*Prunus persica*). — *Physiol. Plant.* 19: 650-659. 1966.
- Farmer, R. E., Jr.: Cottonwood flowering as related to cold requirement of flower buds. — *For. Sci.* 10: 296-299. 1964.
- Kramer, P. J.: Effect of variation in length of day on growth and dormancy of trees. — *Plant Physiol.* 11: 127-137. 1936.
- Kriebel, H. B. & Wang, Chi-Wu.: The interaction between provenance and degree of chilling in bud-break of sugar maple. — *Silvae Genet.* 11: 125-130. 1962.
- Nienstaedt, H.: Dormancy and dormancy release in white spruce. — *For. Sci.* 12: 374-384. 1966.
- Chilling requirements in seven *Picea* species. — *Silvae Genet.* 16: 65-68. 1967.
- Olmsted, C. E.: Experiments in photoperiodism, dormancy, and leaf age and abscission in sugar maple. — *Bot. Gaz.* 112: 365-393. 1951.
- Olson, J. S., Stearns, F. W. & Nienstaedt, H.: Eastern hemlock seed and seedlings: Response to photoperiod and temperature. — *Conn. Agr. Exp. Sta. Bull.* 620. 1959.
- Overcash, J. P. & Campbell, J. A.: The effects of intermittent warm and cold periods on breaking the rest period of peach leaf buds. — *Proc. Amer. Soc. Hort. Sci.* 66: 87-92. 1955.
- Perry, T. O. & Wang, Chi-Wu.: Genetic variation in the winter chilling requirement for date of dormancy break for *Acer rubrum*. — *Ecology* 41: 790-794. 1960.
- Roberts, B. R. & Main, H. V.: The effect of chilling and photoperiod on bud break in American elm. — *J. For.* 63: 180-181. 1965.
- Romberger, J. A.: Meristems, growth, and development in woody plants. — *U.S. Dep. Agr. Tech. Bull.* 1293. 1963.
- Smith, H. & Kefford, N. P.: The chemical regulation of the dormancy phases of bud development. — *Amer. J. Bot.* 51: 1002-1012. 1964.